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THE ORIGIN AND DEVELOPMENT OF THE LAMELLAE IN COPRINUS MICACEUS

Michael Levine

The question as to the origin and method of development of the gills in the hymenomycetes still remains unsettled. Certain stages are well known and have been many times described and figured and certain general conclusions are widely accepted. For example, that in many forms the gills arise endogenously and that the relative positions of the stipe, pileus and hymenium are the same in the undifferentiated button as in the adult. On the other hand, the question as to the method of origin of the gill cavity, the direction of growth of the gill rudiments and their relation to the stipe and pileus, the differentiation of trama and hymenium, etc., have never been clearly and adequately described. The older literature has been reviewed by Atkinson (1906) and others, and I will note only such points as bear especially on my own observations on *Coprinus micaceus.*

Schmitz (1842) describes the gill cavity in *Agaricus Bulliardi* as an annular cavity separating pileus and stipe. The layer of hyphae connecting the outer margin of the pileus and stipe he called the veil or cortina. It is not clear what he means by veil as compared with the peripheral layer found in *Coprinus micaceus.* Schmitz proposed a theory of development for all pileate species of fungi according to which the organ nearest the substratum in the mature form is the structure first to arise, thus the mycelium precedes the stipe and the stipe the pileus while the hymenophore is formed last. Hoffmann's (1856) description of the development of the carpophore lies at the basis of many of the current accounts of the method of formation of the pileus and hymenium. He describes the young buttons of *Agaricus campestris* as small spheres which elongate owing to the growth of the interior cells perpendicularly upward. The terminal cells now grow out laterally and then turn abruptly downward. The ends of these hyphae form the lamellae primordia. In a later paper (1860) he described sixteen further species of Agaricaceae and still later (1861) he described the development of *Coprinus fimetarius.* Hoffmann noticed that the fungus appears at first in the form of a small white sphere in which a brown-colored central portion, the future pileus, is clearly differentiated. His description of the formation of the lamellae does not in any way differ from his previous description of other angiocarpous forms. The next work of importance that followed Hoffmann's was that of De Bary (1866), who also studied the development of *Agaricus campestris*, *A*. (*Pholiota*) *praecox* and *Coprinus micaceus*. He held that the young carpophore begins as a mass of delicate hyphae of uniform diameter densely interwoven. De Bary does not describe the growth direction of the hyphae. Very early this nodule becomes divided into two parts by the formation of a horizontal annular cavity which appears in longitudinal section as two openings in the upper and inner portion of the undifferentiated mass. The region lying above a horizontal plane through this cavity forms the pileus while that below forms the stipe. The hyphae which form the margin of the pileus are continuous with the superficial cells of the stipe. The layer of hyphae directly above the gill chamber grows into it and forms the lamellae. In *Coprinus micaceus* and *C. fimetarius* the lamellae grow into the gill chamber and in the fully developed carpophore are found in contact with the stipe. De Bary's figures of *C. micaceus* clearly show in young stages the edges of the gills in contact with the stipe, though he does not emphasize their connection with it. For *Amanita muscaria* and *A. rubescens* De Bary observed that in buttons somewhat more than 10 mm. long the hymenium and the lamellae in general are already formed and that the lower and inner margins of the lamellae are continuous with the tissue of the stipe just as the upper margins are continuous with the substance of the pileus.

R. Hartig (1874) practically accepts Hoffmann's views as to the origin of the stipe and pileus. In *Agaricus* (*Armillaria*) *melleus* he finds that the lower surface of the pileus forms an exposed hymenium. A vigorous downward growth of the hyphae now sets in from the upper surface and margin of the pileus and a corresponding upward growth of the superficial hyphae of the stipe thus forming a weft of hyphae or a veil hiding from view the hymenium. This differs from Hoffmann's view only in that the hymenium is formed superficially. De Bary (1884) ten years later was misled into accepting Hartig's view as true for a large number of further types. Atkinson (1914^3) has recently reinvestigated this form and found that in *Armillaria mellea* as in many other species of the Agaricaceae the hymenium is endogenous in origin.

Brefeld (1877) maintained that the carpophore of the Coprini arises from a single cell. This cell is not specially differentiated and Brefeld's main interest was in maintaining that there is no morphological equivalent of the ascogonium of the Ascomycetes in the Basidiomycetes. The carpophore *anlage* is a mycelial hypha which gives rise to a number of branches which intertwine, forming a small mass of coiled hyphae. This mass increases in size and internal differentiation sets in. The whole carpophore is covered by a loose layer of globular cells which Brefeld holds is morphologically equivalent to the volva of the Amanitas and differs only in that in the latter genus the structure is more compact. Brefeld held that the lamellae arise as compact bundles of parallel hyphae, each of which has apical growth. Numerous branches are produced which turn to the right and left to form the hymenium. The growth of the lamellae results finally in the adhesion of their edges to the surface of the stipe. He found in large carpophores of *Coprinus stercorarius* that there are about one hundred and fifty lamellae of which one third are primary, two thirds secondary.

V. Fayod (1889) on the basis of studies on a long series of forms discards Hoffmann's conception of the method of development of the pileus and hymenium. Fayod held that in the upper portion of the spherical button a layer of dense hyphae is differentiated which has the form of an inverted bowl. This dense inner portion Fayod calls the *couche piléogène*. He admits that the pileus widens by lateral growth of the hyphae of this pileogenous mass.

Practically nothing further was done during the fifteen years following Fayod's work, but in 1906 Atkinson again took up the question as to the mode of differentiation of the carpophore, especially the veil and lamellae as found in *Agaricus campestris* var. *Columbia* and *A. campestris* var. *Alaska*. The gill rudiments appear first in a longitudinal median section of the young caropophore as two deeply stained areas. These areas represent the cross section of a heavily stained horizontal ring composed of hyphae which have a very dense protoplasm. This annular layer is the hymenial primordium. The hyphae below this structure rupture and an annular hollow cavity, the gill chamber, is thus formed. The lamellae are formed by a downward growth of hyphae from the hymenial primordium into the gill chamber. In (1914[1]) Atkinson confirmed his observations made on *Agaricus cam-*

pestris by a study of *A. arvensis* and *A. comtulus*. In a longitudinal median section of *A. arvensis* the first indication of any internal differentiation in the carpophore primordium is the appearance of two light areas. These represent the beginning of the annular gill chamber, thus differing from *A. campestris*. Atkinson (1914²) in a preliminary report on the development of *Amanitopsis vaginata* and *Lepiota clypeolaria*, holds with Fayod that the primordium of the pileus is the first to develop in the young carpophore. In *Amanitopsis vaginata* he now finds that the trama is continuous with the tissue of the pileus and the surface of the stipe. There is no internal annular gill cavity. In *Lepiota clypeolaria* as in *Armillaria mellea* (1914³) Atkinson describes the first appearance of the hymenium as two masses of hyphae densely stained in the upper part and on opposite sides of a longitudinal section of a young carpophore. The annular gill chamber is formed and then radial plates of hyphae from the primordium grow into the gill chamber forming the lamellae.

Miss Allen (1906), one of Atkinson's pupils, has studied a number of species of Hypholoma and establishes the endogenous origin of the gills in the several species as against the claims of Hartig for *Armillaria mellea*. Fischer (1909) studied the morphological development of *Armillaria mucida* Schrad. but adds nothing to our understanding of the origin and development of the lamellae and the hymenium.

Beer (1911) also confirms the endogenous origin of the hymenium in three species of Agaricaceae. Zeller (1914) studied the development of *Stropharia ambigua* using young buttons collected in the field. He describes the differentiation of the young carpophore as consisting first in the formation of an endogenous annular rudimentary hymenium. He claims that the pileus is formed later by an upward growth of hyphae from the outer edge of the hymenium primordium so as to form an internal inverted cup-shaped structure below the upper portion of the carpophore. The gill chamber is formed by the sagging of the tissue below the hymenium primordium. The lamellae are formed by the downward growth of radial hyphae. The apical cells of these hyphae spread laterally thus forming a groove along the edge of the gill. The hymenial hyphae arise as branches near clamp connections in the subhymenium but gives no figures in support of his statement. Zeller believes that the formation of the hymenium in all annulate agarics precedes that of the pileus primordium while in other agarics the pileus primordium develops first. Zeller does not make clear what becomes of the upper portion of the young carpophore in the annulate agarics which is present before the development of the hymenium when the so-called pileus primordium is formed.

In studying the nuclear phenomena in the mycelia of a number of pileate fungi I found that *Coprinus micaceus* grows well in culture media and is favorable material for studying the formation of the various structures of the carpophore, particularly the lamellae.

METHODS

The carpophores of *Coprinus micaceus* were collected in great numbers during the summer of 1913 in the vicinity of New York. Petri dishes thoroughly cleaned and partly filled with water were covered with circular pieces of oak tag in which two to three circular openings were made somewhat smaller than the diameters of the pilei. The caps were placed over these openings and the Petri dishes were covered. After six to ten hours when the spores had been sown the caps were removed and the pieces of oak tag covered with spores were likewise taken from the dishes and carefully folded and preserved. In tap water germination occurs in about twenty-four hours. The germinating spores were transferred to pint milk bottles containing various media (*a*) soil in which the plants had been growing; (*b*) soil mixed with horse dung; (*c*) horse dung; (*d*) pieces of wood taken from the same soil; (*e*) beef agar; (*f*) carrot; (*g*) beans; (*h*) beet leaves; (*i*) string beans; (*j*) horse dung agar; (*k*) corn meal agar. From forty to sixty days after inoculation young carpophores appeared on the soil, dung and cornmeal agar media. In cases where the medium became too dry sterilized water was carefully added by means of a pipette.

Buttons were carefully removed from the cultures and fixed. The substratum was teased away and the young carpophores were transferred to vials. In case of the agar media the agar was cut away and buttons and medium together were put in a fixing bath. A number of fixing solutions were used, Bouin's, Merkel's, picro-acetic, and chrom-acetic. The best results were obtained, however, with Flemming's weaker mixture. After twelve to twenty-four hours the material was washed in running water, carefully dehydrated and imbedded in 52° paraffin. Sections $5\,\mu$ to $7.5\,\mu$ in thickness were made. The preparations were stained with iron haematoxylin, eosin, acid fuchsin, and congo red, but principally with Flemming's triple stain.

THE CARPOPHORE PRIMORDIUM.

The facts as to the development of the carpophore which may be regarded as settled are as follows: 1st. The relative positions of the stipe, pileus and hymenium are essentially the same in the undifferentiated button as in the adult. 2d. The endogenous development of the hymenium as shown by Hoffmann, Brefeld, Fayod, Atkinson and others.

The points on which further light is needed are: (1) Does the carpophore originate from a single hypha? (2) The origin and direction of growth of the hyphae that form the pileus. (3) The origin and direction of growth of the hyphae that form the lamellae, especially the hymenium. (4) The method of origin of the gill chambers.

I shall use the terms pileus primordium and pileus fundament as corresponding to the *couche piléogène* of Fayod. As I have noted, carpophores of *Coprinus micaceus* are developed in cultures containing cornmeal agar, soil, horse dung, etc., in from eight to nine weeks. A sparse mycelium of white hyphae appears over the surface of the substratum in a week. After six to eight weeks dark brown rhizomorphs appear growing upon the inner surface of the glass container. In about two or three weeks more small white or slightly grayish buttons may be expected to appear on the rhizomorphs on the glass, below the level of the medium and on the medium itself. After a day or two the buttons expand into the carpophores. Such media as cooked carrot, crushed beet leaves, beans, string beans, or bread soaked in grape decoction produce a dense mycelium but neither rhizomorphs nor carpophores are formed so far as my observation goes. Cornmeal agar cultures in test tubes last longer than those in milk bottles. The moisture is better conserved and the mycelium forms a thick layer over the agar upon which carpophores are formed. Such cultures may be studied directly with the low powers of the microscope. The young buttons develop both on mycelial strands in the agar and on the rhizomorphs. Carpophores from both soil-dung and cornmeal agar media were fixed and sectioned.

I have not been able to determine whether Brefeld is right in claiming that the carpophores of Coprinus take their origin from a single hypha. A longitudinal median section of the youngest carpophore I have studied is shown in *figure* 1. The young button consists of a tuft of hyphae whose direction of growth is markedly upward and somewhat divergent, as figured by Brefeld (1877), for *Coprinus* *stercorarius* and rests on the surface of a compact layer of hyphae which covers the agar. The mycelial layer covering the agar consists of a dense plectenchyma of septate hyphae, the walls of which are gelatinous and stain heavily. The hyphae in contact with the agar are abundantly branched and extend down into it forming a very loose network. These hyphae have thin cell walls and a fine granular protoplasm with nuclei easily differentiated in staining. The appearance of these young buttons suggests that they originate by the upgrowth of numerous hyphae from the mycelium covering the agar. That portion of the core of the button nearest the substratum is very compact and the hyphae here appear to be more abundantly branched. The upper portion of the button consists of a loose, well aerated structure of more or less intertwined hyphae. The hemispherical pads, shown by Strasburger (1884) as marking the presence of the so-called protoplasmic pit connections between hyphal cells are conspicuous. The nuclei in all of these cells are well differentiated by Flemming's triple stain. The nucleoles are ruby red while the chromatin is blue.

The surface of the button consists of a fairly well marked zone of rather straight radial hyphae which arise from the outer cells of the mass. Near the substratum these radial hyphae are short and almost horizontal, at the apex of the button they are vertical. These hyphae branch and make a rather uniform peripheral layer over the central region. Each hyphal filament (*fig.* 2) in the layer is about six to eight cells long and one or two of the outer or terminal cells are slightly larger and spherical or oval in shape and their walls are thick and gelatinous. Brefeld's (1877) account of the peripheral layer of the young carpophore of *Coprinus stercorarius* applies perfectly to that of *Coprinus micaceus*.

PILEUS PRIMORDIUM

A little above the central region of the button and just below the peripheral layer an accelerated growth of intertwining hyphae results in the formation of a denser mass which is the beginning of the pileus. The hyphae forming this mass are narrow, much branched and with dense easily stained cytoplasm. This pileus primordium can be distinguished before the sections are stained by its density as contrasted with the looser middle portion below and the thick walled cells of the peripheral layers. It is very small at first but apparently by the rapid growth and branching of its hyphae it broadens out and soon suggests the outlines of the future cap (*fig.* 3) as shown by Fayod (1889) in a number of agarics. Its development is very regular and results in a hemispherical mass of compact narrow interwoven hyphae. At the same time there is a vertical elongation of the carpophore primordium. In the region immediately below the young pileus this vertical growth leads to the formation of parallel strands of hyphae which become the stipe. The cells of the hyphae in this portion of the carpophore appear to have grown especially in their vertical diameters. Their cytoplasm is not dense but is evenly distributed and stains very faintly in comparison with that of the hyphae in the young pileus. In the basal portion of the young carpophore the hyphae are more or less twisted upon each other and their cells are much shorter. Their cytoplasm is somewhat denser and the nuclei can be more easily differentiated. *Figure* 6 shows the appearance of the hyphae which lie in the mycelium and in the lower portion of the carpophore. These cells are long, and their walls are thick and gelatinous. Their cytoplasm contains large and irregularly scattered vacuoles. The nuclei show clear ruby stained nucleoles and finely granular chromatin. The formation of the hemispherical pileus primordium as Fayod has pointed out divides the young carpophore into three distinct regions, the peripheral layer, the pileus primordium and the tissue which will subsequently form the stipe.

THE HYMENIUM

In a slightly older stage we find the beginning of the differentiation of the hymenium. The development of the hymenial elements seems to begin at or near the lower surface of the densely interwoven mass of hyphae which is to develop into the pileus. The whole carpophore is still oval in outline. There is as yet no indication of narrowing to form a stipe. In vertical section the first indication of the developing gills consists of two dense areas symmetrically placed to the right and left above the center of the carpophore as has been so frequently shown in recent papers. They are distinctly endogenous in origin and lie about one quarter of the distance from the surface to the center of the carpophore. Careful study shows that the hyphal cells in these regions are forming downwardly arched ridges of densely staining palisade cells. These palisade cells it may be noted arise in quite a different fashion than that described by Fischer (1909) for *Armillaria mucida* Schrad. and Beer (1911) for *Clitocybe laccatus*. These authors hold that the hymenium is formed by an inward extension of the subcuticular palisade cells which cover the pileus. In *Coprinus micaceus* we have from the very beginning a series of radially placed ridges consisting of a palisade of hyphal cells. The palisade cells observed here appear long before the so-called subcuticular layer of the pileus is differentiated. These young gill cells are rather long, their walls are thickened and stain somewhat more deeply than those of the cells of the pileus primordium (*fig.* 7). It is not easy to determine whether these palisade cells of the young gills become the basidia directly. It is quite probable that further apical growth and branching lead to the definitive formation of the hymenium.

Figure 8 represents a stage a trifle later. The figure shows a portion of a tangential section of a young button which is still cylindrical or spherical or oblong in shape. The growth of the hymenial palisade layer is toward the surface and progresses proportionately to the increasing width of the primordium of the pileus. At the same time the length of the ridges increases by the formation of new palisade cells from above. It is very clear in this stage that the palisade cells do not enclose the edge of a gill but enclose the notch between two gills, that is, they form in section a V opening doward and not upward. Where the ends of the first formed palisade cells meet a small opening appears representing the beginning of a gill chamber of which a somewhat later stage is shown in *figure* 9. The further development of palisade cells leads to the still further enlargment of the gill chamber. A longitudinal median section of a young gill chamber at this stage can hardly be made thin enough to show these relations clearly. Cross-sections of the forming gills are much more instructive. The tangential section shown in *figure* 8 is in a slightly older stage. Here we have a series of newly formed gill chambers. It is obvious at once that the spaces between the gills are not connected to form a single continuous annular cleft as described by Hoffmann, Atkinson and others. In reality we have here a series of radial gill chambers, one between each pair of lamellae. The hyphae of the trama of each gill run straight through into the stipe below and the pileus above. *Figure* 9 represents the young lamellae with the gill chambers between them on a large scale, showing the connections of the hyphae of the trama. The gill chamber is not altogether empty for some of the hyphae from the stipe seem to branch and grow into it as shown by Atkinson (1914[3]) for *Armillaria mellea*. *Figures* 10, 11, 12 represent hyphae from the trama and stipe in a somewhat later stage; two nuclei are found in each cell. The character of the branching and the continuity of the stipe and gill hyphae are clearly shown.

We have then in the differentiation of the pileus and the upper portion of the stipe region of *Coprinus micaceus* first the formation of a palisade layer of ridges of cells for each pair of hymenial surfaces which line the cavity between two adjacent gills. The gills are strictly endogenous in origin. There is no general annular gill cavity as described by Hoffmann, De Bary, Atkinson, and others, and no annular hymenial primordium.

As the horizontal diameter of the carpophore increases we find that the differentiation of the pileus and lamellae progresses centrifugally. As the growth progresses the distances between the lamellae primordia increase and new gill primordia arise between the old ones as shown in *figure* 13.

Further Development of Pileus and Stipe

The peripheral layer of the pileus which was originally composed of cylindrical hyphae capped by one or more oval cells now becomes modified. The cylindrical cells of the earlier stages become oval. Stages shown in *figures* 8, 13 represent later stages in the development of the pileus. The peripheral layer is now made up of a few cylindrical cells nearly all of which are globular and gelatinous. The change in form takes place from the outer toward the inner cells as Brefeld (1877) described. The thickness of the layer is greater over the apex of the pileus and decreases as it approaches the base of the young carpophore. The structure of the pileus proper has undergone a marked change. The fine compactly coiled hyphae seen in the earliest stages have become much less compact so that the individual cells are more distinct. The hyphae widen and the spaces between them become larger. They are nevertheless still intertwined and show no definite direction of growth. In the lower central portion of the pileus which lies in close proximity to the stipe region the hyphae also interlace yet many may be traced directly into the stipe below while others may be traced directly upward to the periphery of the pileus. The hyphae near the upper surface of the pileus give rise to short, stubby, vertical branches consisting of a longer terminal cell and one or two shorter ones below. These branches lie parallel to each other and form a palisade layer over the pileus (*fig.* 15) below the outer peripheral layer. This structure is similar to that described by Fayod (1889) and later by Fischer (1909).

In many cases the nuclei in these cells are well differentiated and both the nucleoles and chromatin granules are visible. The hyphae found in the portion of the pileus over the lamellae are oriented and appear to be growing downward; still in many well stained sections hyphae are also found growing downward as indicated by the direction of the branching. In somewhat later stages the flesh of the pileus is made up of broad septate hyphae having a sparse granular cytoplasm in which two nuclei are regularly present. The lamellae are still continuous with the tissue of the stipe below just as they are with the pileus above. The hymenial surface is sharply differentiated and distinct basidia and cystidia are recognizable. There are no basidia formed on the edges of the gills, as shown by Brefeld for other species of Coprini.

Figure 8, a longitudinal tangential section very close to the median, represents best the structure of the stipe at this stage. The basal portion consists of a compact intertwining mass of hyphae (*fig.* 5) from which the hyphae of the center of the young stipe arise. The hyphae in the stipe which lie exterior to the central region are still continuous with the hyphae in the young gills. As we approach the outer layer of the stipe, that is, the layer just below the peripheral layer of globular cells we find the hyphae become narrow. The density of the cytoplasm and the thickness of the cell walls make this a well differentiated layer. These hyphae can be traced into the pileus where they are continuous with the cells of the surface there. The growth direction is upward as shown by the character of the branching. The further development of the stipe consists primarily in the vertical elongation and swelling of the hyphae in the outer and middle layer of the stipe. A cross section of the young stipe shows that there are two types of hyphae, the wide and the narrow, similar to those which have been described by Harper (1902) for *Coprinus ephemerus*, although at this stage the broad type predominates. The cells in these hyphae are long as compared to their width and have a homogeneous cytoplasm in which a large number of nuclei are found (*fig.* 16). The nuclei are clustered and lie in the center of the cell.

The increase in size of the stipe is accompanied by the increase in size of the primordia of the lamellae and an outward and downward growth and expansion of the pileus. The hyphae in the upper portion of the stipe near the pileus are intertwining and septate and two or three nuclei are invariably found in each cell as shown in *figure* 18.

The significance of this structure is not clear, although it may be the point of origin of secondary growth in the pileus as suggested by Miss Allen (1906).

SUMMARY

1. The carpophore primordium of *Coprinus micaceus* arises from the mycelium directly or from a rhizomorph. The young button makes its appearance from forty to sixty days after either cornmeal agar or soil media are inoculated with spores.

2. The pileus initial appears as a hemispherical mass of fine, narrow, interlacing septate hyphae having a dense cytoplasm which stains heavily with Flemming's triple. The peripheral layer of cells of the carpophore primordium is differentiated very early in that they stain more deeply.

3. The primordium of the hymenium arises at or near the lower surface of the pileus primordium and appears in vertical section as two densely stained areas of palisade cells, symmetrically placed to the left and right above the center of the carpophore primordium.

4. A palisade of hyphal cells is formed pointing obliquely downward so as to form a series of arched ridges. These ridges form the young gills. The hymenial elements do not enclose the edge of a gill but enclose the notch between two gills.

5. The small opening formed at the point where the first formed palisade cells meet is the beginning of a gill chamber. The further development of palisade cells leads to the enlargement and further development of the gill chamber.

6. Longitudinal tangential sections show the gill chambers in series, one gill chamber between each pair of lamellae. The hyphae of the trama of each gill run straight through into the stipe below and the pileus above.

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EXPLANATION OF PLATES XXXIX AND XL

The figures in Plate XL were drawn with the aid of the camera lucida from preparations stained with Flemming's triple stain. Leitz 1/16 objective and No. 1 ocular were used in making figures 9 and 15; the rest of the figures on this plate were made with the 1/16 objective and No. 3 ocular. Distance from camera lucida to drawing board 90 mm. Microphotograph 1 was made with Leitz objective No. 6 and ocular No. 3; 3, 8, 13 and 17 were made with objective No. 3 and ocular No. 3.

Cramer's micro-ray filter No. 7 was used.

PLATE XXXIX.

FIG. 1. Vertical median section of an undifferentiated carpophore, on agar. × 250.

FIG. 3. Vertical median section of young carpophore in which the pileus primordium is differentiated, on agar. × 170.

FIG. 8. Vertical tangential section showing arched palisade tissue and a series of gill chambers. × 285.

FIG. 13. Vertical tangential section of a somewhat older button showing a series of gills with separate and independent gill chambers between them. Secondary gills alternating with the primary gills. × 85.

FIG. 14. Portion of figure 13 enlarged, showing (*a*) primary gills, (*b*) gill chamber, (*c*) pileus, (*d*) secondary gills, (*e*) hymenium, (*s*) stipe.

FIG. 17. Section of a stipe in a well-differentiated carpophore, showing nuclei clustered in the center of the cell. × 120.

PLATE XL.

FIG. 2. Hypha from the peripheral layer in the young carpophore.

FIG. 4. Hyphae from the basal portion of the young carpophore.

FIG. 5. Same as figure 4, but later stage.

FIG. 6. Hypha from the mycelium near base of young carpophore.

FIG. 7. Part of a vertical tangential section of a young carpophore showing ridges of palisade cells which form gill primorida.

FIG. 9. Part of a vertical tangential section of a carpophore somewhat older showing the palisade cells of the hymenium and two of a series of gill chambers. The hyphae of the trama are continuous with the hyphae of the stipe below and the pileus above.

FIG. 10. Hyphae from the trama showing branching upward.

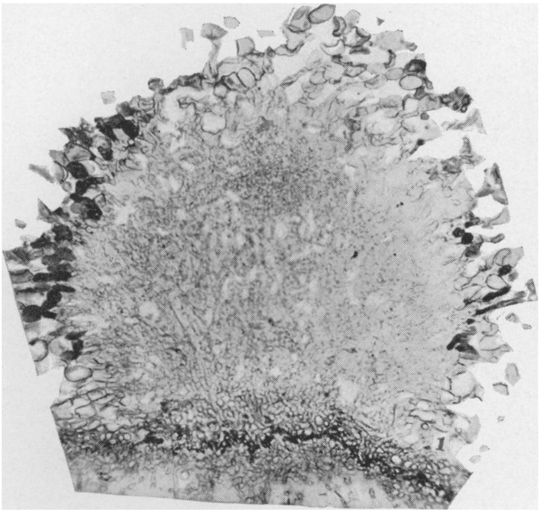
FIG. 11. Other cells from the trama.

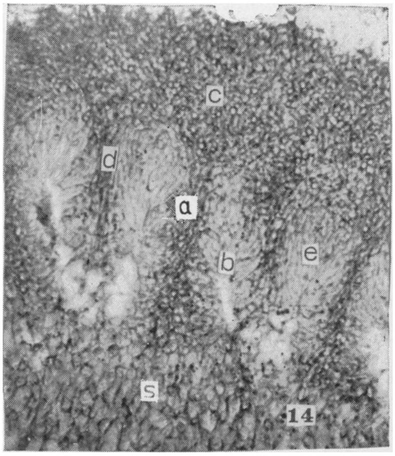
FIG. 12. Hyphae from the stipe which connect above with the hyphae of the trama such as are shown in figures 10 and 11.

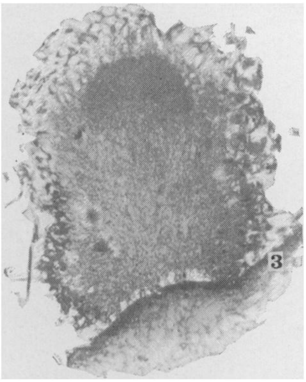
FIG. 15. Part of the upper portion of the pileus showing the palisade arrangement of the cells below the peripheral layer.

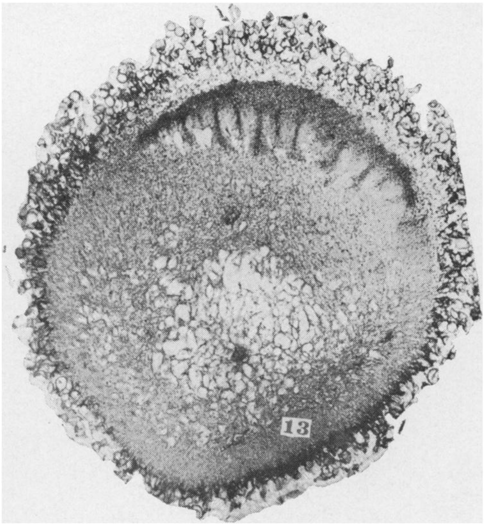
FIG. 16. Cells from the portion of the stipe shown in figure 17, enlarged, showing numerous nuclei.

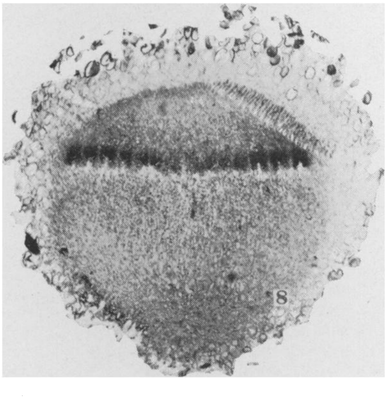
FIG. 18. Hyphae from the upper portion of the stipe near the pileus in a well differentiated carpophore.

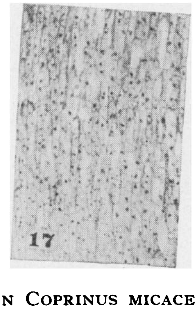




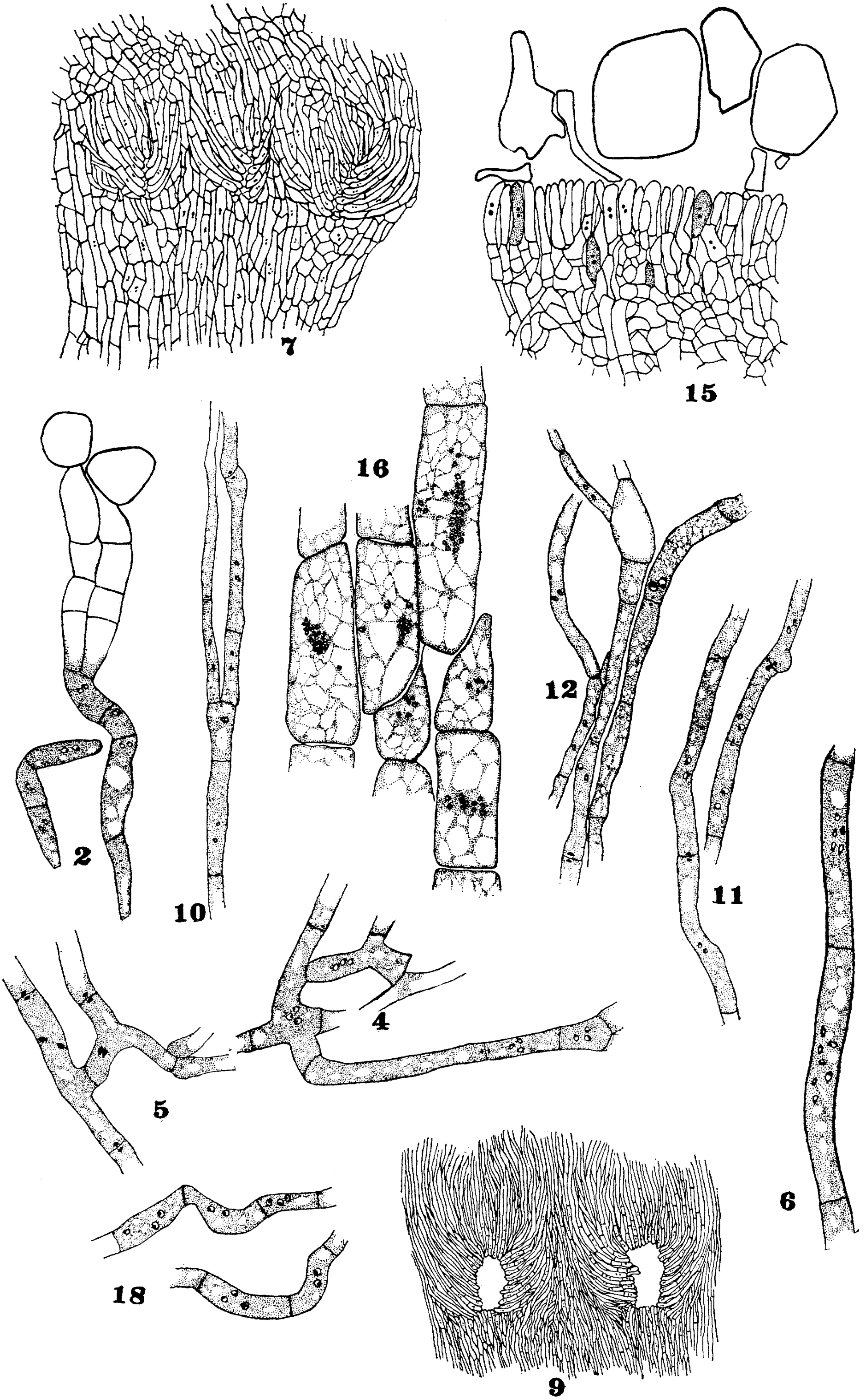








LEVINE: ORIGIN OF LAMELLÆ IN COPRINUS MICACEUS.



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